

Smolt Transformation in Two California Steelhead Populations: Effects of Temporal Variability in Growth

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Abstract.—We tested the effect of temporal patterns in food supply on life history decisions in coastal steelhead *Oncorhynchus mykiss irideus* from a Central California coastal (CCC) population (Scott Creek) and a Northern California Central Valley (NCCV) population (upper Sacramento River basin). We manipulated growth through feeding experiments conducted from May to the following March using warm (2006 cohort) and cool (2007 cohort) temperature regimes. Survival in seawater challenges just before the time of typical juvenile emigration provided an index of steelhead smolt versus nonsmolt life history pathways. Survival varied significantly with fish size (with larger fish being more likely to survive than smaller fish) and by source population (with CCC steelhead being more likely to survive than NCCV steelhead of the same size). The timing of increased food supply (treatment group) did not significantly affect seawater survival rates in either NCCV or CCC steelhead. For both strains, the eventual survivors of seawater challenges (putative smolts) diverged from the eventual mortalities (putative nonsmolts) in both size and growth rate by June in both years, suggesting that the initial growth advantages were maintained throughout the experiments. A significant divergence in condition factor between smolts and nonsmolts by December matched the expected morphological transition of smolts, which showed faster growth in length than weight compared with nonsmolts. The apparent timing of the decision window, several months before the typical period of smolt emigration, matches the patterns observed for other salmonids. In coastal California, this decision must occur

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before fish have had the opportunity to take advantage of improved winter–early spring feeding conditions. These results support the role of early growth opportunity in life history decisions and provide insight into the applicability of life history models for managing California steelhead.

Intraspecific diversity in life histories of coastal steelhead *Oncorhynchus mykiss irideus* (anadromous rainbow trout) and coastal rainbow trout represents a remarkable adaptation to the variable environment of Pacific North America (Behnke 2002a). Some individuals complete their entire life history in freshwater whereas others, sympatric at birth, spend variable amounts of time in both freshwater and the ocean before returning to freshwater to reproduce. Thus, coastal steelhead and rainbow trout are considered to be a single subspecies with two forms, one anadromous (steelhead) and the other resident (rainbow trout; Behnke 2002b). Understanding the origin, maintenance, and relationships between anadromous and resident forms is important in basic and applied salmonid biology, the latter particularly in the context of altered flow regimes on managed rivers.

The expression of alternative life histories is the result of a complex interaction between genetic variation, including local adaptation, and environmental conditions. In addition, since the physiological machinery required for life in freshwater and the ocean is distinctly different, smolting and residency–maturation entail development conflict (Thorpe 1987).

Atlantic salmon *Salmo salar* also exhibit a wide range of intraspecific life history variation, and a relatively well developed conceptual and computational theory exists to describe this variation (see Thorpe et al. 1998; Mangel and Satterthwaite 2008, and the references therein for more details). According to this life history theory, the developmental pathways (smolt transformation and maturation) followed by salmonids are determined by responses to growth conditions at particular times of the year (called decision windows) and expected survival rates associated with each developmental pathway. The responses themselves are threshold traits and the thresholds are genetically determined. In this manner, there is a natural gene–environment interaction determining life history variation, and the theoretical framework couples proximate and ultimate factors that shape life histories. This framework has also been applied to Arctic char *Salvelinus alpinus* (Rikardsen et al. 2004) and more recently to steelhead in California (Satterthwaite et al. 2009, 2010).

In laboratory experiments rearing Atlantic salmon, Metcalfe et al. (1988, 1989) found that growth rate, size, and dominance rank observed in the first summer after emergence were significantly and predictably correlated with life histories assumed the following

spring. They concluded that both larger and more dominant, faster growing Atlantic salmon are more likely to undergo smolt transformation and metamorphose into the sea-going phase after only 1 year in freshwater compared with their smaller or subordinate slower-growing siblings, which remain in freshwater habitat for at least another year. These results support the notion that disparate life histories assumed by individuals of the same sibling group are determined within a decision window at least 8 months before emigration and smolt transformation. Due to the similarity between Atlantic salmon and steelhead life history (i.e., iteroparity, high variation in expression of life histories), similar processes might be expected to govern steelhead life history trajectories.

Within the geographic range of steelhead, the environment and growth opportunities vary substantially. For example, steelhead in northern California's Central Valley experience good growth conditions (e.g., adequate food and suitable temperatures) year-round, whereas central California coastal steelhead exhibit minimal growth in summer and fall and depend on growth opportunities associated with increased flow in winter and spring (Merz 2002; Hayes et al. 2008; Sogard et al. 2009). Due to variation in first-year growth between the Northern California Central Valley and central California coast, the timing of the decision window and the correlation between growth and the likelihood of smolt transformation at age 1 may also differ between regions.

The natural variation in first-year growth across seasons and the biogeography of California steelhead allowed us to investigate local adaptation with respect to temporal variation in growth and smolting decisions. In addition, the similarity in life history strategies between steelhead and Atlantic salmon motivates biologists to investigate the influence of decision windows in smolt transformation. Similar to the results derived in the laboratory experiments of Metcalfe et al. (1988, 1989), we predict that both larger and more dominant, faster growing steelhead will be more likely to undergo smolt transformation and metamorphose into the sea-going phase after only 1 year in freshwater compared with their smaller or subordinate slower-growing siblings, which probably remain in freshwater habitat for at least another year. In addition, we predict that steelhead in temperate California climates, particularly in coastal streams, will delay their life history decision as long as possible to allow them to assess their energetic state after the potentially productive

winter–spring growth period. In contrast to Atlantic salmon, whose size at the time of emigration is largely dependent on growth during the previous summer and fall, steelhead in California have the opportunity to markedly increase in size during the months just before expected emigration. We examine competing hypotheses concerning life history strategies of steelhead, decision windows, and the effects of growth and local adaptation in the context of the following hypotheses:

H_1 : Seawater survival (i.e., smolting) is determined by fish length or condition upon seawater entry, not a decision window, with similar requirements in all strains. For this hypothesis we assume that smolt metamorphosis is essentially instantaneous, depends on size and morphology alone, and leads to the prediction that there will be an effect of fish size or condition on seawater survival regardless of variation in temporal growth patterns.

H_2 : Seawater survival is instantaneously determined by fish length or condition upon seawater entry, but the morphological requirements for seawater survival vary as a function of local adaptation. This hypothesis leads us to predict that survival, as a function of morphology, will differ significantly between steelhead of different strains or regions.

H_3 : There is a decision window for smolt transformation that occurs between emergence and seawater entry, with similar requirements in all strains. This hypothesis leads to the prediction that there will be an effect of fish state (size, condition, growth rate) during a limited time interval on subsequent seawater survival, and the threshold state will be similar among strains.

H_4 : There is a decision window for smolt transformation that occurs between emergence and seawater entry; however, the timing of the decision window will differ between strains as a consequence of regional differences in temporal growth patterns. This hypothesis leads to the prediction that there will be an effect of fish state (size, condition, growth rate) during a limited time interval on subsequent seawater survival and the effect will be specific to region of origin.

Study Regions

We compared two steelhead populations, one from the Northern California Central Valley (NCCV) and the other from the central California coast (CCC), reared in a common-garden experiment (Garland and Adolph 1991) to investigate possible adaptation to local environments. Each population was tested under two different temperature regimes, warm and cool, to test for interactive population and temperature effects on growth and subsequent life history decisions. Temperatures followed natural season progressions and were within the range experienced by steelhead in

California, but the warm regime averaged 4°C higher than in the cool regime. Our reason for selecting NCCV and CCC steelhead strains was based on the difference in their rearing environments and our interest in possible effects of local adaptation on smolting decisions. The NCCV fish came from Coleman National Fish Hatchery, which was established in 1942 on Battle Creek, a tributary of the northern Sacramento River and part of the Central Valley steelhead Distinct Population Segment (DPS; USFWS and NMFS 1996). Most steelhead-producing streams in the Sacramento River watershed are fed from snowmelt. However, most are also regulated by dams, leading to altered flow regimes and moderated temperatures, thus, possibly altering historic growth opportunities (McEwan 2001). We assume fish from Battle Creek are an adequate proxy for NCCV steelhead and that they have had the opportunity to adapt to the seasonal temperature regimes and growth patterns characteristic of the region. The CCC fish came from the Monterey Bay Salmon and Trout Project hatchery, established in 1982 on Scott Creek, part of the Central California Coast DPS. In contrast to many of the rivers in the NCCV region, CCC watersheds are typically much smaller, undammed, and largely regulated by precipitation, thereby maintaining naturally fluctuating flow and temperature regimes. Laboratory experiments involving steelhead from these regions provide excellent test cases to investigate adaptation to local environments due to the dissimilarity of their natal environments.

Methods

Source populations.—The spawning programs of the Coleman National Fish Hatchery and the Monterey Bay Salmon and Trout Project hatchery differ in methodology. For the latter, wild winter-run steelhead are collected and transported directly to a small conservation hatchery on Scott Creek. These fish are identified as wild by the presence of an adipose fin (all hatchery-origin smolts have this fin removed before release). It is possible that some fish in our experimental cohort were F_2 progeny of hatchery-origin adults, as hatchery-origin fish are allowed to spawn in the watershed. Steelhead returning from the ocean and spawned in the Coleman National Fish Hatchery are predominantly of hatchery origin, although the gametes from both wild and hatchery-origin steelhead are present and mixed during artificial fertilization.

Experimental protocol.—In 2006, we transferred CCC steelhead (fork length [FL] = 44.5 ± 5.1 mm [mean \pm SD]) from the Monterey Bay Salmon and Trout Project hatchery to the laboratory during the second week of June, and NCCV steelhead (FL = 39.7

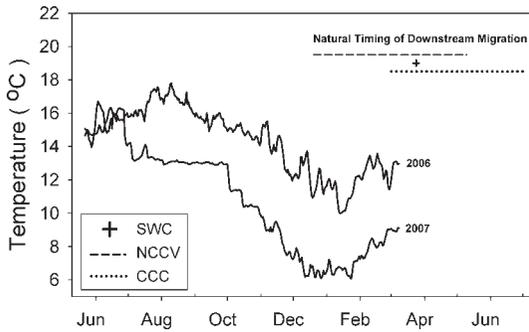


FIGURE 1.—Daily water temperatures in laboratory tanks during coastal steelhead growth experiments in 2006 and 2007. The cross marks the date (March 24) of the seawater challenge (SWC), the dashed and dotted lines the timing of natural downstream migration observed in both Northern California Central Valley (NCCV) and central California coastal (CCC) steelhead populations.

± 3.0 mm) from the Coleman National Fish Hatchery in the third week of May. In 2007, we transferred both NCCV steelhead (FL = 36.4 ± 3.1 mm) and CCC steelhead (FL = 43.8 ± 3.2 mm) in the second week of May. We randomly assigned fish to 16 cylindrical tanks (92 cm diameter, 490 L) with 20 fish per tank and eight tanks of each strain. Strains were maintained separately throughout the experiments. A continual flow of oxygenated freshwater pumped through the aquarium system supplied comparable water quality among tanks. Pieces of polyvinyl chloride (PVC) pipe within each tank provided structural habitat.

Fish received rations of hatchery fish pellets (Bio-Oregon, growth formula) ad libitum in May and June to facilitate acclimation to the aquarium system. In July, all tanks were placed on low rations to restrict growth. The 16 tanks were assigned to four treatment groups with two replicate tanks per strain. Ration levels were adjusted over time as a function of body size, temperature, and treatment (see Table A.1 in the appendix); food was distributed once per day. Fish received low rations except during the treatment period, when they received eight continuous weeks of rations ad libitum daily. Treatment periods were as follows: treatment 1, August 1–September 26; treatment 2, September 27–November 22; treatment 3, November 23–January 18; and treatment 4, January 19–March 16. Our objective was to provide fish with a diet supporting moderate but restricted growth except for an 8-week period of rapid growth opportunity. Fish on low rations were fed on 4 d a week. On nonfeeding days, fish received *Spirulina* algae to maintain relative gut fullness and limit hunger-based aggression. Before we initiated the experiments, we established, with a

subset of fish not included in the experiments, that *Spirulina* was a low quality food that did not support growth but was readily consumed.

We used two different temperature regimes, warm (2006 cohort) and cool (2007 cohort), which was comparable with seasonal temperature cycles in California (Figure 1) to test for interactive population and temperature effects on growth and subsequent life history decisions. Water temperatures cooler than ambient were produced by an air-cooled in-line water chiller (Aqua Logic, Inc.). Photoperiod was controlled by an automatic light system to match that within the Scott Creek area (latitude, 36.97°N). Gradual transitions in light level mimicked dawn and dusk patterns.

We initially marked all fish with elastomer tags (Pacific Northwest Technology) to identify individuals. As they attained 65 mm FL, fish were tagged with passive integrated transponder (PIT) tags (Allflex Corporation). All fish were measured monthly for FL and total weight. We checked tanks daily for mortalities, and siphoned tanks to remove feces and other waste material. In 2006, we added fish to tanks that had high initial mortality before the initiation of the first feeding treatment. All supplemental fish had been maintained on *Spirulina* algae for several weeks before being added to the experimental tanks. These fish represented a small number of individuals ($n = 13$) and were supplemented to maintain social interactions within a tank; because we did not have initial measurements for these fish, we did not include them in statistical analyses. We accrued mortality throughout the experiment in both strains and both years from a number of causes (e.g., stress and cannibalism). In December we reduced the maximum number of fish per tank to 15 to avoid crowding and maintain water quality. We selected excess fish at random and euthanized them with tricaine methanesulfonate (MS-222).

At the conclusion of the final treatment period in March, we tested fish in a seawater challenge to determine osmoregulatory capacity. We scheduled our seawater challenge to best fit the overlap in the natural timing of downstream migration observed in these populations (Figure 1; McEwan 2001; Hayes et al. 2004). Fish were slowly acclimated ($1^\circ\text{C}/\text{h}$) to the temperature of our seawater aquaria (13.1°C in 2006, 11.5°C in 2007) then transferred directly from the freshwater tanks to large ocean-fed seawater tanks (salinity, 35‰) and checked every 6–12 h for mortalities. The seawater challenge lasted approximately 3 weeks and was terminated after five consecutive days passed without producing additional mortality. Fish were not fed during the challenge period.

Analysis.—Results of seawater challenges allowed us to partition individuals into life history pathways of emigration (smolts) or a more protracted freshwater residency (non-smolts). We identified survivors of the seawater challenge as smolts and fish that did not survive as non-smolts. We expected to identify decision-window timing based on differential survival probability among the four temporal feeding treatments. In addition, we expected a temporal divergence of Fulton's condition factor, K (Fulton 1904), in smolts because the transition from parr to smolt is typically accompanied by a decrease in K (Wagner 1974; Tipping et al. 1995; Thorpe et al. 1998). A divergence in K between smolts and non-smolts in advance of the time of emigration would also support the hypothesized decision window for a life history pathway. We used absolute growth in length (mm/d) for comparisons among strains, years, and treatments. Absolute growth was overall more independent of initial fish size than were other metrics (i.e., specific or instantaneous growth), which agrees with other assessments supporting the use of length as the measure of growth in juvenile salmonids (Sigourney et al. 2008).

Four fish in 2006 and five fish in 2007 extruded milt during measuring events before the seawater challenge and were identified as mature males based on ripe testes. Because these individuals adopted a separate life history exclusive of our study comparisons, they were excluded from all analyses. Dissection of all fish after the challenges verified that all other fish were immature. All immature fish that were present in the tanks for the initial measurement and survived to the final measurement before seawater challenges were included in statistical analyses.

Seawater survival.—We constructed a generalized linear model (GLM) of seawater survival (with SYSTAT 11) to assess the probability of seawater survival at a given size for each strain in each year, modeling survival as a binomial response with a logit-link function. We analyzed the probability of seawater survival as a function of FL at seawater entry, treatment, strain, and the strain-by-treatment interaction.

Divergence of K .—We calculated fish condition using Fulton's K as follows: $K_i = 10^5 \times W_i/L_i^3$, where W_i is the mass (g) and L_i is the FL (mm) of the i th fish. We compared growth rates and Fulton's K for smolts and non-smolts using repeated measures analysis of variance (ANOVA) for each strain and year, followed by univariate F -tests comparing monthly results.

Growth performance and trajectories.—General growth comparison between years and strains was evaluated with a two-way ANOVA using mean growth rates per tank averaged across the complete time series.

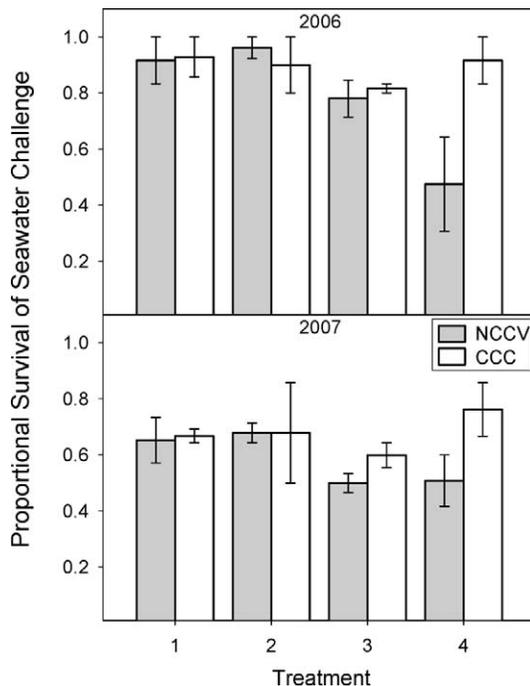


FIGURE 2.—Proportional survival of steelhead from the seawater challenges by feeding treatment, year, and strain. The error bars indicate the minimum and maximum survival of duplicates within each treatment.

To assess the effectiveness of increased ration levels during treatment periods, we compared growth rates between fish receiving rations ad libitum and all other fish, which were receiving moderate rations, using one-way ANOVA with a Bonferroni adjustment for multiple tests.

Results

Survival in Seawater Challenges

Survival after direct transfer to seawater differed by year and strain (Figure 2). In 2006, 90.8% of 76 CCC steelhead survived the seawater challenge, compared with 76.8% of 99 NCCV steelhead. In 2007, survival overall was lower, with 68.2% of 107 CCC and 58.8% of 114 NCCV fish still alive after the seawater challenge. The proportional survival of fish subjected to the seawater challenge within each treatment differed by strain. There was a decrease in survival of the NCCV strain for treatment 4 in 2006 and for treatments 3 and 4 in 2007, but there was no clear pattern of survival among treatments for the CCC strain in either year (Figure 2). However, we did not detect a significant effect of treatment or a strain \times treatment interaction on the probability of seawater survival for either year in our GLM. Because treatment and the

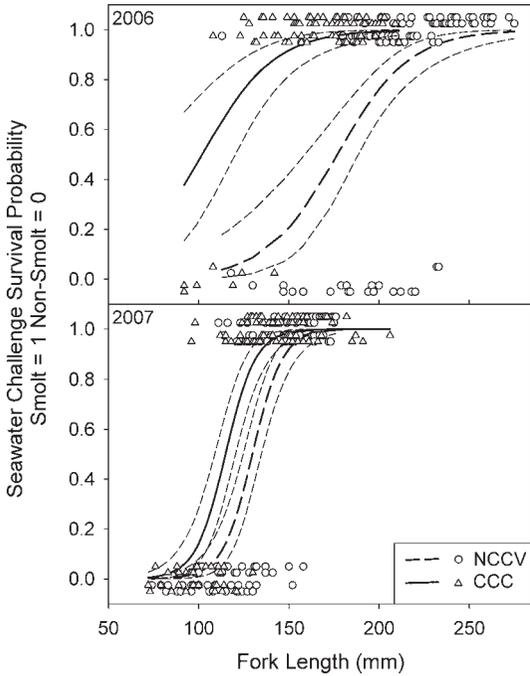


FIGURE 3.—Logistic regressions of survival probability against final fork length from 2006 and 2007 seawater challenges for NCCV and CCC steelhead by individual fish. Size and strain were significant determinants of survival ($P < 0.001$) in each year. The fine dashed lines show the 95% confidence intervals of the logistic plots.

strain \times treatment interaction were insignificant we ran a logistic regression model with just strain and length as predictor variables. Fish length was a highly significant determinant of survival for both strains ($P < 0.001$), with larger fish more likely to survive than smaller fish (Figure 3). Within each year the size required for 50% probability of survival in seawater significantly differed between strains ($P < 0.001$). In 2006 CCC steelhead reached a 50% likelihood of surviving the seawater challenge at 104 mm FL, compared with 177 mm for NCCV fish. In 2007 CCC steelhead reached a 50% survival probability at 115 mm and NCCV fish at 130 mm.

Divergence of K

In 2006 there was no clear significant difference in the condition factor, K , between smolts and nonsmolts, although smolts had consistently lower mean K from October (NCCV fish) or December (CCC fish) through the end of the experiment (see Discussion). In 2007, however, a significant divergence in K of smolts versus nonsmolts was detected (Figure 4). The initial K of eventual smolts in both strains was significantly higher

than that of nonsmolts (univariate F -tests following repeated measures ANOVA: $P < 0.001$), although K values subsequently converged and then diverged. Beginning in November for CCC fish and December for NCCV fish, the difference in K reemerged but in a new direction, with smolts having significantly lower K than nonsmolts (Figure 4). This difference continued through March, just before the seawater challenge for both strains. Thus, fish that presumably adopted an emigration life history followed the expected pattern for fish undergoing smolt transformation, with greater growth in length than weight, resulting in lower K values than that observed for nonsmolts by the end of growth trials.

Growth Patterns

Overall growth during the experiments was faster in NCCV fish compared with CCC fish (ANOVA on tank means: $F_{1,28} = 34.9, P < 0.001$) and faster in 2006 than 2007 ($F_{1,28} = 34.9, P < 0.001$). A significant interaction between strain and year ($F_{1,28} = 12.2, P = 0.002$) reflected the greater difference between years for the NCCV strain compared with the CCC strain. The NCCV fish responded to the presumably enhanced growth opportunity provided by warmer temperatures and increased food availability in 2006 to a much greater extent than did CCC fish. In 2006, NCCV steelhead maintained faster growth throughout the experiment and were, on average, 48 mm longer than CCC fish at the time of seawater challenges (Figure 5) and 75 mm longer than NCCV fish in 2007. The CCC fish, in contrast, exhibited a more moderate response to the enhanced growth opportunity, with final sizes in 2006 averaging only 31 mm longer than in 2007.

Growth significantly accelerated during ad libitum ration periods for both strains and all treatment periods in both 2006 and 2007 (all $P < 0.05$ after Bonferroni adjustments for multiple tests) with the exception of the December treatment period of the CCC strain in 2006. On average, NCCV fish growth increased by 127% with ad libitum rations in 2006 and by 95% in 2007 compared with growth rates on restricted rations. For the CCC strain, growth increased by 60% in 2006 and by 102% in 2007 for fish receiving rations ad libitum.

Growth and Condition Trajectories of Smolts and Nonsmolts

Growth rates of eventual smolts were faster than those of eventual nonsmolts throughout the experiments (Figure 6). Life history pathway significantly influenced growth rate within each strain and year (repeated measures ANOVA: all $P < 0.001$). Comparison of mean growth between smolts and nonsmolts at each measurement time (univariate F -tests) suggested a rapid

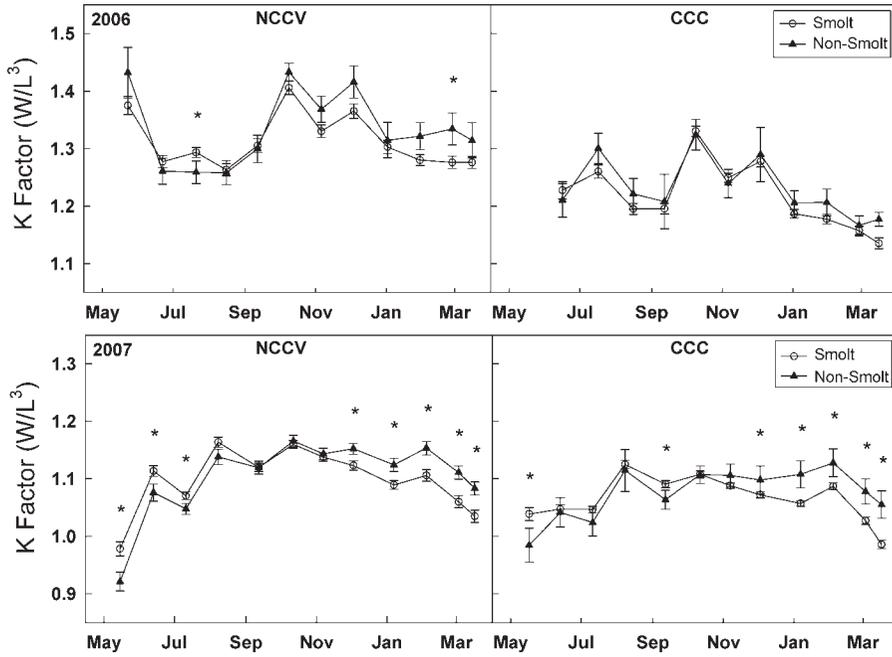


FIGURE 4.—Change in Fulton's K over time among NCCV and CCC steelhead smolts and nonsmolts from the 2006 and 2007 experiments. The error bars denote SEs. Asterisks indicate significant differences between smolts and nonsmolts based on univariate F -tests (all $P < 0.05$) following repeated-measures ANOVAs conducted within each strain \times year group.

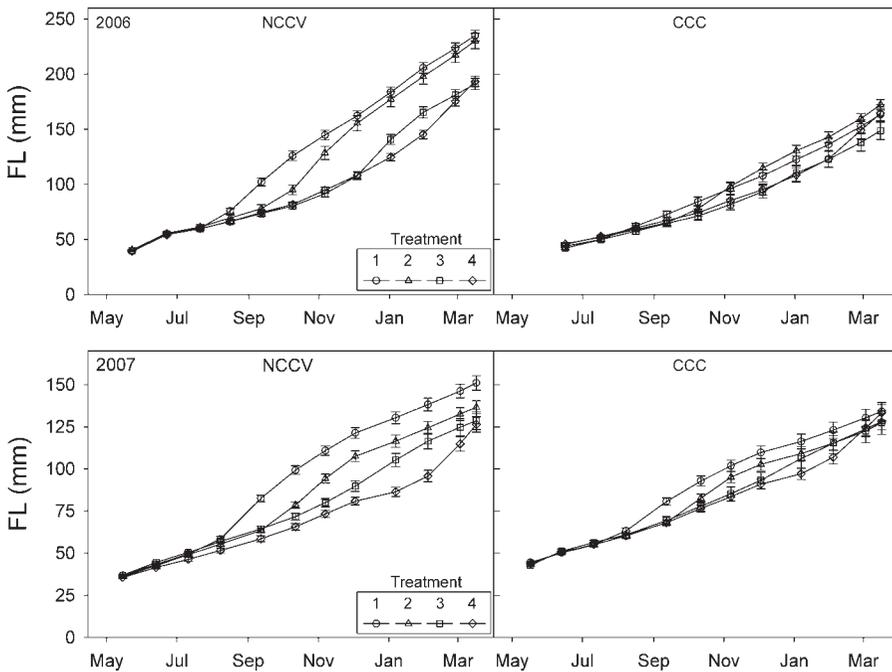


FIGURE 5.—Mean fork lengths (mm) of juvenile steelhead from the NCCV and CCC strains by feeding treatment and month during growth experiments conducted in 2006 and 2007. The error bars represent SEs.

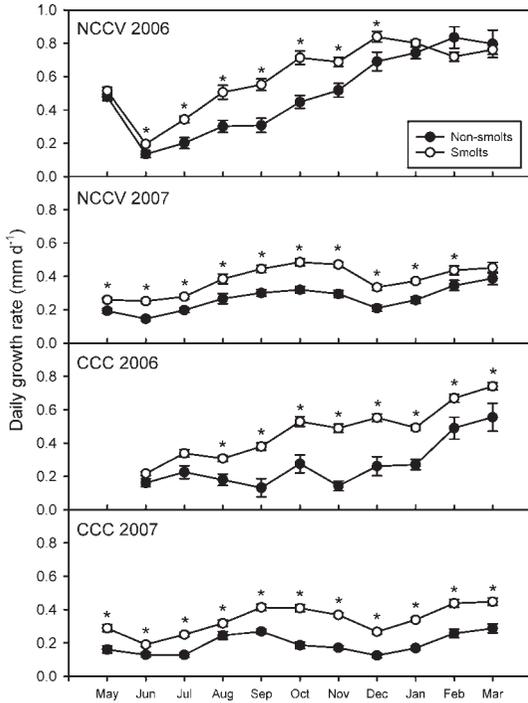


FIGURE 6.—Mean growth rates of juvenile steelhead from the NCCV and CCC strains following the smolt and nonsmolt life history pathways during growth experiments conducted in 2006 and 2007. The error bars represent SEs; the asterisks indicate significant differences between life history based on univariate *F*-tests (all *P* < 0.05) following repeated-measures ANOVAs conducted within each strain × year group.

divergence in growth rate before our treatments began. Significantly faster smolt growth continued to the end of the growth period for CCC fish in both years, but in NCCV fish an apparent convergence was noted, with reduced smolt growth, accelerated nonsmolt growth, or both in the final time periods.

On average, across all time periods and both strains, nonsmolts grew 33% more slowly than did smolts. In some time periods the differences were dramatic, with growth of nonsmolts being up to 65% lower than that of smolts during the same time period and with the same ration level.

The contrasts in growth between life history trajectories resulted in rapid divergence of size distributions (Figures 7, 8). For both strains in both years, eventual smolts were larger than eventual nonsmolts at the first measurement in May (univariate *F*-tests following repeated measures ANOVA: all *P* < 0.001). By November of both years, segregation in sizes was clearly evident and continued to the end of experiments in March.

Discussion

Growth Contrast

There were obvious differences in the growth rates between steelhead strains from each region and between 2006 and 2007. In general, NCCV fish were able to maintain higher growth rates than did CCC fish, and displayed a larger difference in growth capacity in the warmer temperature regime (2006) relative to CCC fish. Overall, it appeared that NCCV fish capitalized on enhanced growth opportunities from either increased food availability or increased temperatures and showed markedly increased growth rates, whereas CCC fish had a more moderate response.

Central coast streams typically have low water flows and relatively low food availability compared with Central Valley systems. As such, the growth opportunity for NCCV fish in natural conditions is likely to be far greater than that of CCC fish during most the year, particularly during the summer months, thereby allowing fish to achieve larger sizes at age 0. As an extreme example, the average length of age-0 steelhead in December is approximately 200 mm FL in the American River and approximately 70 mm in both Soquel and Scott creeks (S. M. Sogard and coworkers, unpublished data). Ocean survival is strongly correlated with size at ocean entry (Ward et al. 1989; Bond et al. 2008). It is possible, then, that NCCV fish consistently experience increased growth opportunity while CCC fish do so much less frequently; thus, the former are selected in their natal environment for emigration at age 1 while the latter are not. Central coast fish, in contrast, appear to emigrate primarily at age 2 after spending a second summer and winter in freshwater (Shapovalov and Taft 1954). Fish from the Scott Creek population clearly have the capacity to grow quickly, as they exhibit growth rates of greater than 1 mm/d in the warm food-rich habitat of the lagoon estuary (Hayes et al. 2008). Our results suggest that in the laboratory environment, CCC fish exhibited risk-averse behavior and did not take full advantage of the growth opportunity provided by warm temperatures and high food levels.

It is important to note that growth rates induced during restricted feeding treatments still exceeded growth rates under natural CCC summer and fall conditions, a period when growth is barely positive (Hayes et al. 2008; Sogard et al. 2009). We were not able to simulate the extremely poor growth conditions of CCC summer and fall periods in the laboratory. As a consequence, CCC fish overall were larger at age 1 than they would be in the natural system of Scott Creek. The high proportion of smolts in each of our CCC laboratory cohorts further supports the role of

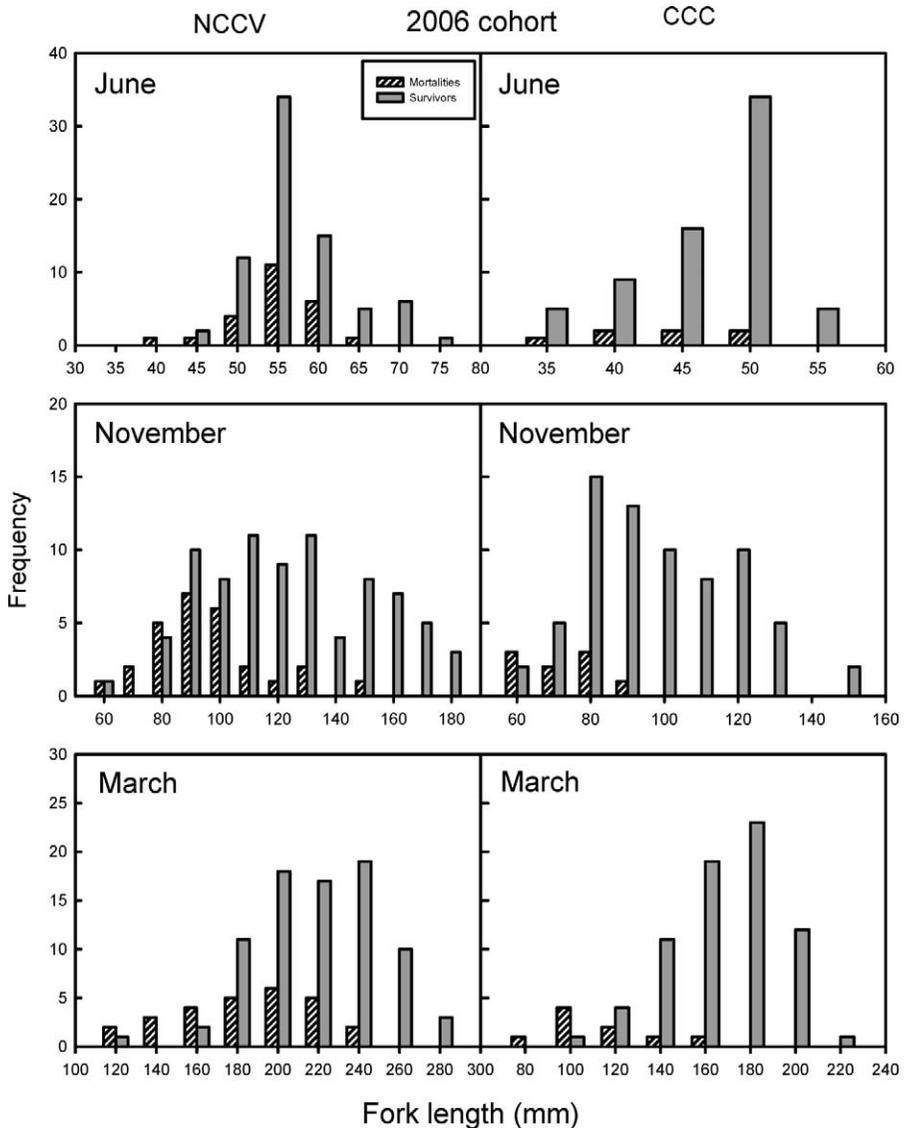


FIGURE 7.—Size-frequency distributions of NCCV and CCC strains of juvenile steelhead from the 2006 cohort at the beginning, middle, and end of laboratory growth experiments, divided into eventual smolts (survivors) and eventual nonsmolts (mortalities).

early growth on the emigration decision. Under the natural low food conditions in Scott Creek, age-1 emigration from upstream habitats is rare, with most fish requiring at least an additional year in freshwater before smolt transformation.

We observed a marked difference in fish behavior between the two strains, which may underlie the contrasts in observed growth. In both cohorts (2006 and 2007), NCCV fish were generally more active compared with CCC fish. The NCCV fish were

aggressive during feeding and appeared to actively use the entire water column of the tanks. In contrast, the CCC fish spent considerable time at the bottom of tanks using the PVC shelter and were slow to respond to the presence of food pellets. The differences in behavior and growth in a common environment suggest local adaptation in these traits.

For the NCCV strain, it is not possible to determine whether this local adaptation reflects the source population or is a function of hatchery selection.

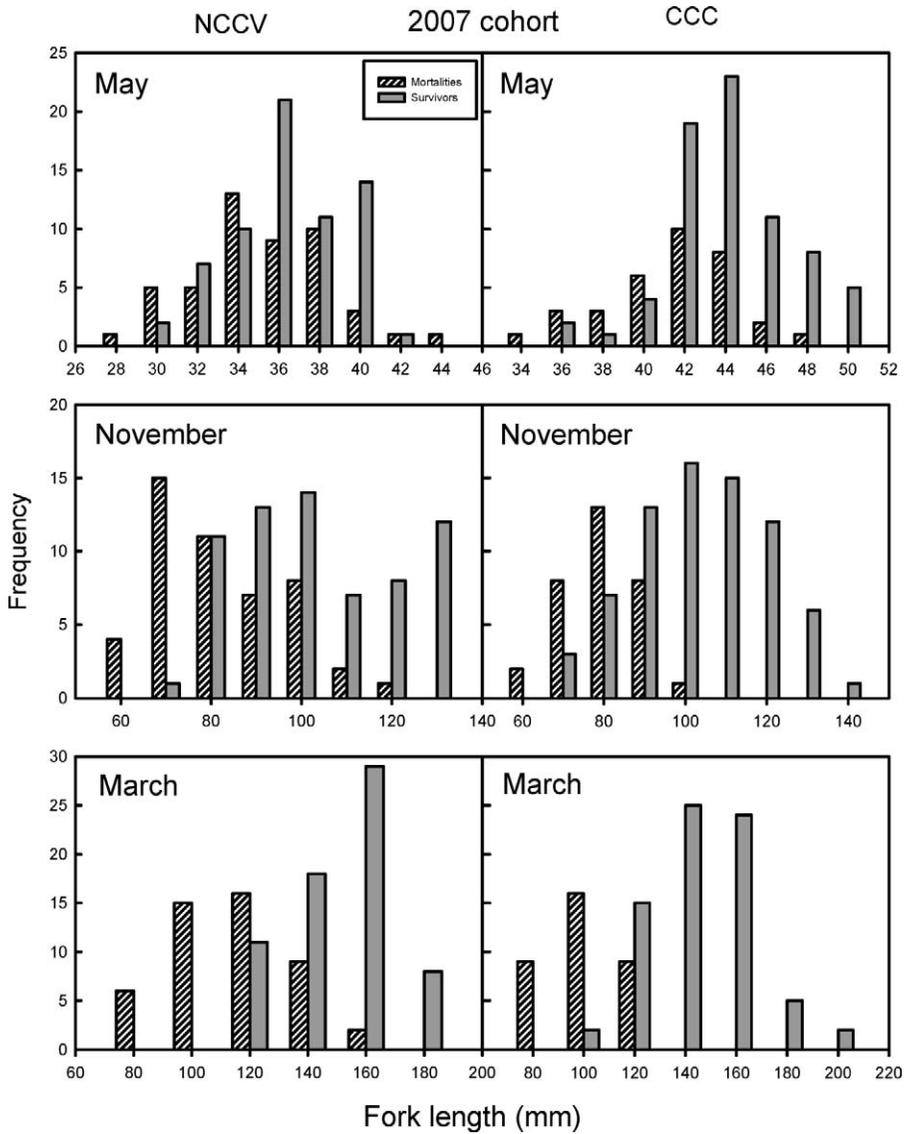


FIGURE 8.—Size-frequency distributions of NCCV and CCC strains of juvenile steelhead from the 2007 cohort at the beginning, middle, and end of laboratory growth experiments, divided into eventual smolts and eventual non-smolts.

Coleman National Fish Hatchery uses primarily hatchery-origin fish in their spawning program, which allows for selection of hatchery-favored traits such as aggressive feeding behavior (see Weber and Fausch 2003 for a review of domestication effects on salmonid behavior). The Scott Creek hatchery spawns only wild adults, limiting the likelihood of such selection. Future study is needed to distinguish between these explanations. Regardless, these results demonstrate an intriguing difference in growth strategy between the two populations.

At the individual level, both strains had high variability in growth within replicate tanks. The coefficient of variation ($100 \times \text{SD}/\text{mean}$) of FL averaged 8% within a tank at the beginning of experiments in May–June and 18% for the last measurement in March. The consistently faster growth rates of smolts compared with that of non-smolts throughout the experiment could arise either from inherent differences in growth capacity or behavioral aspects of competition. Juvenile steelhead exhibit high levels of aggression in laboratory environments

(Abbott and Dill 1985) and relatively small size differences can determine dominance (Berejikian et al. 1996). Our results are similar to those of Metcalfe et al. (1989), with apparent early establishment of dominance leading to a higher probability of adopting the emigration pathway at age 1.

Decision Window

Manipulation of the timing of accelerated growth opportunity (the four temporal high-ration treatments) and analysis of survival did not clearly identify a specific time period for a smolt transformation decision window in either year or strain. We acknowledge that the precise timing of the window (along with the timing of the ultimate migration event) may vary among years based on environmental conditions and among individuals based on genetic thresholds (Thorpe et al. 1998). However, the significant divergence of K values between smolts and nonsmolts appeared to begin in November for both strains in 2007, suggesting the adoption of an emigration pathway well before the expected emigration period, and a decision window before the winter. Similar (but nonsignificant) patterns were apparent in K for both strains in 2006, which lends support for rejecting H_1 .

Although results of the treatment comparisons were inconclusive, it seems apparent that the steelhead begin smolt transformation and switch to the smolting pathway no later than November. Thus, the decision window occurs before the season of good growth opportunity (particularly for coastal populations) in winter and early spring. This was counter to our expectation that steelhead in temperate California climates would delay the life history decision as long as possible compared with salmonids in colder climates with minimal growth opportunity in winter.

The early divergence in growth of smolts and nonsmolts, before our separation of fish into treatment groups, suggests that steelhead may have been on a particular developmental pathway shortly after emergence. We speculate that not only are steelhead adopting a life history pathway in the fall, the condition of fish soon after emergence can significantly affect which pathway is adopted, either due to a decision made at that time or due to its effect on growth rate for the remainder of the fish's life and, thus, its size at a later decision window. These results support accepting H_3 or H_4 and are consistent with similar findings for Atlantic salmon (Metcalfe et al. 1989; Thorpe and Metcalfe 1998; Thorpe et al. 1998), suggesting that California steelhead follow similar developmental pathways.

Local Adaptation

We could not identify the exact timing of the decision window from our results. As a consequence we could not formally address H_4 . However, our results did illuminate some striking and surprising differences between strains. The seawater challenge showed substantial differences in the size threshold for smolting between NCCV and CCC fish, which supports accepting the local adaptation component of H_2 and H_4 . We propose that the disparity in size thresholds for seawater survival between strains is a consequence of regional differences in growth opportunities and indicative of local adaptation. During the early juvenile rearing period, summer and fall, instream growth opportunity is high in NCCV regions in contrast to CCC regions, in which growth opportunity is restricted. In addition, average annual growth in CCC regions is lower compared with NCCV regions. This reduced growth opportunity could result in CCC fish adapting physiological capacities for seawater tolerance at smaller sizes if the net risk of ocean emigration at smaller sizes is less than the net risk of waiting to emigrate at a later age (Satterthwaite et al. 2009). Another possibility is that the CCC fish are simply preparing for seawater tolerance and not necessarily ocean emigration. Bond et al. 2008 have shown that CCC steelhead often emigrate downstream to continue rearing in coastal estuaries where growth opportunity increases tremendously (Hayes et al. 2008). The speculation that CCC fish are adapted for early seawater entry or smolt transformation at smaller sizes is consistent with the prediction of a smaller threshold size for smolting in CCC fish compared with NCCV fish (Satterthwaite et al. 2009, 2010).

Seaward emigration and seawater tolerance in salmonids can be altered via hatchery practices and parentage (Shrimpton et al. 1994; Hill et al. 2006). One could argue that some of the differences observed between strains in our experiments were a function of differing hatchery practices rather than evidence of adaptation to local environments. It is still essential to recognize that the populations of NCCV and CCC steelhead we examined are remarkably different strains naturally reproducing in dissimilar environments. The fundamental distinction of these two California strains provides evidence of adaptation to local environments, including hatchery management, and this contrast has important implications in evaluating how life history expression can differ between populations.

Conclusion

This study implies that life history models similar to those developed for Atlantic salmon can be applied to

steelhead (Mangel and Satterthwaite 2008; Satterthwaite et al. 2009). Our results provided compelling evidence for the existence of a decision window and the influence of early development in life history expression of steelhead. In addition these results support the likelihood of local adaptation, resulting in a tremendous degree of variation in the growth potential, behavior, and physiological capacities of California steelhead. Therefore, it is imperative that early development is considered in future research focused on life history expression, and that the integrity of currently established Distinct Population Segments is maintained across the biogeographic range of this species.

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Appendix: Feeding Regimes for California Steelhead

TABLE A.1.—Ration levels fed to steelhead (NCCV and CCC) during 2006 and 2007 experiments. Ration volume was calculated as a percentage of the total biomass in each tank. The high ration levels were set to ensure that fish were feeding to satiation. When residual food was determined to be excessive or insufficient, we adjusted the ration levels (see footnotes). Single asterisks indicate that food was distributed 5 d a week, double asterisks that food was distributed 4 d a week.

Period	2006		2007	
	High ration	Low ration	High ration	Low ration
May 1–31	5.0		3.0	
Jun 1–2	5.0*		2.0**	
Jun 3–28	5.0*		3.0**	
Jun 29–31	2.0**		3.0**	
Aug 1–26	4.0	2.0**	4.0	2.0**
Sep 27–Oct 22	4.0	2.0**	4.0	2.0**
Oct 23–Nov 5	4.0 ^a	2.0**	4.0	2.0**
Nov 6–28	4.0	2.0**	4.0	2.0**
Nov 29–Dec 17	4.0	2.0**	2.0	1.0**
Dec 18–28	6.0, 5.2 ^b	2.0**	2.0	1.0**
Dec 29–Jan 1	6.0, 5.2 ^c	2.0**	2.0	1.0**
Jan 2–5	4.0	2.0**	2.0	1.0**
Jan 6–9	3.0	2.0**	2.0	1.0**
Jan 10–25	3.0	2.0**	2.5	1.0**
Jan 26–Feb 20	3.0	2.0**	3.0	1.0**
Feb 21–28	3.0 ^d	2.0**	3.0	1.0**
Feb 28–Mar 5	3.0	2.0**	3.0	1.0**
Mar 6–16	3.0 ^e	2.0**	3.0	1.0**

^a NCCV, +2 g; CCC, +1 g.

^b Different amounts for NCCV, CCC.

^c NCCV, –2 g; CCC, –1 g.

^d NCCV, –2 g (one of two tanks).

^e NCCV, –2 g; CCC, –1 g.